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Deadwood and saproxylic beetle diversity in naturally disturbed and managed spruce forests in Nova Scotia

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Abstract

Even-age industrial forestry practices may alter communities of native species. Thus, identifying coarse patterns of species diversity in industrial forests and understanding how and why these patterns differ from those in naturally disturbed forests can play an essential role in attempts to modify forestry practices to minimize their impacts on native species. This study compares diversity patterns of deadwood habitat structure and saproxylic beetle species in spruce forests with natural disturbance histories (wind and fire) and human disturbance histories (clearcutting and clearcutting with thinning). We specifically examine how beetle diversity differs in relation to disturbance history and how beetle variation is linked to the diversity of deadwood habitats. Beetle and deadwood data were collected from thirty spruce forests in Nova Scotia and analyzed under three related diversity perspectives: alpha (diversity within local forests); beta (heterogeneity among local forests within disturbance classes); and gamma (cumulative species richness within disturbance classes). Few data support a prediction of lower alpha deadwood and beetle diversity in managed forests, or a prediction of lower gamma species richness in managed forests. The beta scale analysis yielded support for the following two hypotheses: (1) beetle assemblages are different in forests with different disturbance histories; (2) turnover of beetle assemblages is higher among naturally disturbed forests than among managed forests. The prediction of lower gamma diversity of saproxylic beetle species in managed forests compared to naturally disturbed forests was not supported. The lack of differences between naturally disturbed and industrial forests in structures that are characteristic of older forests (e.g., large-diameter deadwood) may relate to the presence of residual deadwood in second growth forests lingering from before clearcut harvesting. However, such residual deadwood is only an artifact that will soon decay and not be replaced. This suggests that the continuity of deadwood microhabitats for species that depend on old-forest structures is only short-term.

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Keywords
Saproxylic, Coleoptera, deadwood, forest management, disturbance history, Nova Scotia, Canada

Introduction

Disturbance is one of the main determinants of ecosystem structure, composition, and function (Pickett and White 1985; Attiwill 1994; Abel and Stepp 2003). A major concern with respect to biodiversity loss in forest ecosystems is driven by the threat that disturbance imposed by modern forestry has on species diversity through altering the habitat structure (Haila and Kouki 1994; Haila et al. 1994; Siitonen 2001; Langor et al. 2006). Deadwood substrates serve as microhabitats that host an immense diversity of forest species (called saproxylics), primarily invertebrates (Speight 1989; Warren and Key 1991; Siitonen 1994, 2001, 2003; Grove 2002). Unfortunately, the physical diversity of deadwood in forests has a high potential for being altered by modern forestry practices. Many saproxylic species are threatened due to loss of habitat (Siitonen 2001, 2003; Jonsson et al. 2005; Larsson et al. 2006, Langor et al. 2006). Thus, considering the fate of saproxylic species and their deadwood microhabitats in industrial forests is an essential part of any forest management initiative that values native species conservation and ecologically sustainable resource use (e.g., Canadian Council of Forest Ministers 1995; National Board of Forestry Sweden 1996; Canadian Forest Service 1997; Siitonen 2001; Langor et al. 2006).

The diversity of deadwood substrates (abundance and richness of physical states) is often changed when natural disturbances are replaced by forestry disturbances (Gore and Patterson 1986; Hagan and Grove 1996; Sturtevant et al. 1997; Siitonen 2001; Langor et al. 2006). Whereas natural disturbances occur stochastically, forestry is deterministic (Attiwill 1994) and aimed toward specific economic ends, namely, the maximization of sustainable fiber productivity. Over recent decades, industry and government in Canada and across the globe have favored even-age management practices of clearcut-replanting or clearcut-regeneration with thinning. Natural disturbances have therefore been largely replaced by even-age forestry.

We predicted several changes to the local diversity of deadwood substrates in human disturbed forests. Even-aged harvesting practices may drive (1) the loss of large diameter deadwood due to short time-spans of stand rotations; (2) a decreased local diversity of deadwood decay structures due to all deadwood being in a single decay cohort which senesces through even-aged stand cycles; (3) the loss of standing deadwood due to the view that standing deadwood is a source of economic inefficiency and a safety hazard; and (4) the loss of deadwood from the many native tree species that are selected against because they are not considered economically valuable.

We examined saproxylic beetles (Order Coleoptera) diversity patterns and relationships with deadwood diversity patterns in managed and naturally disturbed spruce (*Picea rubens* Sarg. or *Picea mariana* Mill., Pinaceae) forests in Nova Scotia, Canada. Many species have highly specialized saproxylic niches (Speight 1989; Warren and Key

1991; Siitonen 2001; Langor et al. 2006), suggesting that species assemblages should be sensitive to variation in deadwood substrates. That most saproxylic beetles can be easily sampled using relatively inexpensive methods (Økland 1996) favors the group logistically as well as ecologically.

This study takes an exploratory look at a system that has only recently begun to receive detailed attention in North America (Hammond et al. 2001, 2004; Langor and Spence 2006; Langor et al. 2006). In the Maritime Provinces of Canada only Kehler et al. (2004) and Dollin et al. (2008) have previously examined saproxylic beetle communities in detail. Our basic objective is to identify whether modern forestry is generating invertebrate diversity patterns that are different from those generated by natural disturbances. This task can be approached on many scales and from many perspectives on species diversity. Specifically, we adopt a three-part view on species diversity, similar to the alpha, beta, and gamma diversity perspectives proposed by Whittaker (1972). Alpha diversity pertains to local diversity or, in our case, diversity measured at the scale of a single forest stand. Beta diversity pertains to the turnover of alpha diversity between or among localities; in other words, the degree to which alpha diversity differs from locality to locality. At the beta scale, we compare the turnover of species and deadwood diversity among local forests within four disturbance history classes (see methods). We use gamma diversity to refer to the total number of species cumulatively sampled within all forests in each disturbance history class.

We conceptualized and tested the following set of specific predictions for the alpha, beta, and gamma scales:

Alpha scale:

(1) naturally disturbed forests exhibit higher local diversity of deadwood (habitat) structures than forests that are under even-age management regimes; and (2) local diversity of saproxylic beetle assemblages within forests is proportional to the heterogeneity of deadwood habitat structures within forests; and thus (3) naturally disturbed forests exhibit higher local diversity of saproxylic beetle species than forests that are under even-age management regimes.

Beta scale:

(1) beetle assemblages and forest structures are different in forests with different disturbance histories, which is to say that species and deadwood compositions are more similar within forest disturbance classes than among forest disturbance history classes (see methods); (2) heterogeneity in deadwood habitat structures is higher among naturally disturbed forests than among forests that are under even-age management regimes; and (3) turnover of saproxylic beetle species among forests is proportional to the heterogeneity of deadwood habitat structures among forests; and thus (4) turnover of saproxylic beetle species is higher among naturally disturbed forests than among forests that are under even-age management regimes.

Gamma scale:

(1) the cumulative beetle species diversity across all naturally disturbed forests is higher than the cumulative beetle species diversity across all forests under even-age management regimes.

Methods

Study forests. Thirty spruce forests were selected for beetle sampling in central Nova Scotia, Canada, concentrated in two regions: the Liscomb Game Sanctuary (45° 09′ N, 62° 30′ W) and an area north of St. Margaret's Bay (44° 44′ N, 63° 54′ W). The forests were chosen to represent one of four general disturbance histories, two anthropogenic and two natural: (1) clearcut origin (CC), (2) clearcut origin followed by pre-commercial or commercial thinning (CC+), (3) fire disturbance origin (F), and (4) wind disturbance origin (W). We set several criteria for the experimental forests. Canopy trees had to be numerically dominated (70 % minimum) by spruce (*Picea* spp.). Stands had to be large enough to contain a 40 × 120 m trap-sampling grid with a surrounding 100 m buffer (minimum of 7.7ha in total size) to limit edge effects from riparian areas, forests of different tree species composition, and any non-forested areas, including recent clearcuts. The closest two centers within forest were 800 m apart while the most distant two were separated by 190 km. Stands were in addition selected to reduce as much as possible geographic spatial dependence. Time since last intense disturbance (clearcut, fire, severe hurricane, etc.) was limited to a minimum of 30 years, as indicated by mean age of dominant canopy trees. Of the selected forests, mean stand ages ranged from 30 to over 250 years. A concentration of thinned forests in the young age range reflects the recent implementation of thinning as a management practice. Forest management in Nova Scotia was not strictly regulated and private woodlots constituting 75% of the province could be managed as the owners saw fit when the present study stands experienced their last disturbance. Thus, rotation ages vary greatly and the selection of stands could not be controlled with regard to ages of stands or specific management regimes applied. Clearcutting, however, is the standard practice but subsequent silvicultural practices vary (Nova Scotia DNR 2000).

The concentration of wind disturbed forests in the older age range reflects the fact that wind disturbance in Nova Scotia is generally of low intensity, allowing trees to become much older than does short-rotation forestry disturbance. Managed forests were common and thus chosen randomly from a larger subset of forests; the rarity of naturally disturbed spruce forests, on the other hand, allowed no room for random selection. Table 1 shows the distribution of the study forests among disturbance history classes and age classes. It is evident that a rigorous sampling design with regard to stand age and disturbance was not possible to achieve and has been addressed in the analysis (see Analysis).

The remaining three forests were fire origin and dominated by black spruce (*Picea mariana*), a species dependent on fire for regeneration when not in lowland or bog soils (Fowells 1965). Black spruce and red spruce are known to hybridize and they are often difficult or impossible to distinguish (Roland and Smith 1969).

Forest habitat structures. In each study forest, deadwood volume and crown closure were sub-sampled in six 15 × 15 m plots located at 40 m intervals along two parallel transects spaced 40 m apart. For each piece of deadwood, the length and diameter at each end were measured (or estimated) to calculate volume based on the frustum of a cone. Tree species and decay states (see Table 2) were recorded for each piece of deadwood to allow independent tallying of deadwood in different classes. To

Table 1. Distribution of forests delineated by age and disturbance history classes.

Disturbance History Classes	Class Codes for Reference	Mean Canopy Tree Age		
		30–49 years	**50–69 years**	**70 years +**
clearcut origin	CLEARCUT	1	6	4
clearcut and subsequently thinned	CC&THINNED	6	2	0
naturally disturbed (fire origin)	FIRE	1	2	1
naturally disturbed (wind only)	WIND	1	2	5
total		**9**	**11**	**10**

estimate percent crown closure, two methods were used. In most forests, a flat mirror with 20 equally spaced dots was held horizontal at chest level to determine the proportion of dots occurring in crown-covered space. In remaining forests, a short cardboard tube was used as a scope to visually estimate proportions of crown closure. Applying both methods in one forest to test comparability returned similar results. Three crown closure readings were taken at random distances (10–20 m) from each of the six plot centers through late July to early August (during peak deciduous foliage). Within each plot, a healthy dominant canopy tree was cored to estimate tree age for a total of six trees per forest. Descriptions of all variables measured are given in Table 2.

Beetle sampling and identification. To sample saproxylic beetles systematically at each forest, a window flight intercept trap (FIT) design was employed. The FIT is passive in that it does not attract beetles, thus providing random samples of the fauna that actively fly in the local environment. Økland (1996) showed that window FITs were effective for providing large samples of saproxylic beetles and Wikars et al. (2005) showed that window FITs compared with other methods caught the greatest number of species. In a single season Muona (1999) found that FITs collected 50.6% of the species of beetles (and 48.3% of forest species) in a study in the Oulanka region of Finland. Emergence traps where beetles are sampled as they emerge from experimental logs (Gibb et al. 2006) are logistically difficult. This was not a popular method for sampling saproxylic beetles in the field when this study was conducted in 1997 and thus, was not considered an option for this study.

We employed a design consisting of two bisecting 30 × 30 cm transparent plastic (Lexan 0.030) panes, covered with a white plastic (Styrene 0.040) conical roof for rain shelter, and attached to a Styrene collecting funnel below. Removable plastic sample jars attached at the base of the collecting funnel held a 50 % diluted ethylene glycol killing/preserving solution. In each forest site, six FITs were hung from existing tree branches, with the bottom of the trapping surface approximately 1 m above the forest floor. FITs were located 40 m apart along two parallel transects separated by 40 m.

All FITs were set up during 13–19 May 1997 and run until 13–15 August 1997. Catches were collected every two weeks within 3 days of each other, and the ethylene

Table 2. Description (A) forest structure variables measured in each forest, (B) deadwood diversity and (C) beetle diversity attributes.

Variable Name	Description
(A) CROWN	crown closure (%)
SIZE1	volume of deadwood with diameter 0–15 cm (m^3 /100m^2)
SIZE2	volume of deadwood with diameter 16–30 cm (m^3 /100m^2)
SIZE3	volume of deadwood with diameter >30 cm (m^3 /100m^2)
DECAY1	volume of deadwood with little or no decay (m^3 /100m^2)
DECAY2	volume of deadwood with 1–5 cm decay depth (m^3 /100m^2)
DECAY3	volume of deadwood with >5 cm decay depth (m^3 /100m^2)
STANDING	volume of deadwood standing, > 45° from floor (m^3 /100m^2)
FALLEN	volume of deadwood fallen, < 45° from floor (m^3 /100m^2)
DECIDUOUS	volume of deadwood in all deciduous species (m^3 /100m^2)
CONIFER	volume of deadwood in all coniferous species (m^3 /100m^2)
ALLDWOOD	volume of all deadwood measured (m^3 /100m^2) (the summation of deciduous and coniferous deadwood)
(B) SHAN-SIZE	Shannon diversity index of deadwood in 3 size classes
SHAN-DECAY	Shannon diversity index of deadwood in 3 decay classes
SHAN-POS	Shannon diversity index of deadwood in 2 position classes (standing and fallen)
SHAN-D/C	Shannon diversity index of deadwood in 2 tree type classes (deciduous or conifer)
SHAN-ALL	Shannon diversity index of all 10 deadwood classes (above)
(C) ABUNDANCE	total number of beetles from all species sampled
RICHNESS	total number of beetle species sampled
RICH/ABUN	richness/abundance of all beetles in each site
SHANNON	Shannon diversity index of all beetles in each site
RARE-1	number of species sampled at site for which the total catch was 1 individual
RARE-5	number of species sampled at site for which the total catch was 5 or fewer
RARE-10	number of species sampled at site for which the total catch was 10 or fewer
RARE-15	number of species sampled at site for which the total catch was 15 or fewer
RARE-30	number of species sampled at site for which the total catch was 30 or fewer
RARE-60	number of species sampled at site for which the total catch was 60 or fewer

glycol solution was changed at this time. This gave six two-week samples for each trap, with the collection dates on or adjacent to 3 June, 16 June, 1 July, 13 July, 30 July, and 14 August. Beetles were separated from each trap sample within one week and preserved in 70% acetic ethyl alcohol.

All beetles were identified to species although only species considered to be saproxylic were employed in subsequent analyses. Saproxylic (*sensu lato*) is defined here in accordance with Speight (1989). The inclusion of species in this category was made on a specific or, more commonly, generic basis, consulting a wide variety of published sources (commencing with Arnett and Thomas (2000) and Arnett et al. (2002), followed by family-specific treatments), or if such information was not readily available in the literature, consulting with specialists of different Coleoptera families listed in the acknowledgments. Appendix 1 gives the full list of saproxylic species caught.

Species identifications were initially made by D.J. Bishop employing the reference collection of the Canadian National Collection of Insects, Arachnids, and Nematodes. Subsequently the process of identification was continued by C.G. Majka and employing the reference collection of the Nova Scotia Museum. At both stages the process was greatly assisted by Coleoptera specialists (listed in the acknowledgments) who were able to identify difficult species or confirm determinations done by Bishop or Majka. The general systematics and taxonomy follow Arnett and Thomas (2000) and Arnett et al. (2002).

Statistical analyses. The aim of the initial analysis was to test whether habitat structures differed according to the four disturbance history classes: (1) clearcut, (2) thinned, (3) fire, and (4) wind. For this, distribution-free Kruskal-Wallis tests (non-parametric analogs to one way analysis of variance) were used, followed by the Numenyi *a posteriori* multiple comparison tests in cases where the initial tests suggested a significant ($p<0.05$) difference (described in Zar 1999).

To test predictions at the alpha scale, the initial procedure was to reduce the structural information and the beetle assemblage from each forest to meaningful diversity attributes. The Shannon diversity index (Brower et al. 1990) was selected to index both entities.

The Shannon diversity value was calculated independently for four aspects of deadwood habitat diversity for each forest: (1) decay classes, (2) size classes, (3) standing/fallen classes, and (4) conifer/deciduous classes. The Shannon diversity for measures of beetle assemblage was calculated without refinement (Table 2).

The habitat diversity and beetle assemblage attributes were independently tested for any differences with respect to disturbance history using parametric, one-way ANOVA tests, with Tukey HSD multiple comparison *post hoc* tests to detect the location of any significant ($p<0.05$) differences between any two disturbance history classes. Taking the measures of the beetle assemblage to be the dependent variables and the forest habitat diversity variables as the independent variables, stepwise multiple linear regression analysis (Weisberg 2005) was used to test if and how aspects of the beetle assemblage were related to deadwood habitat heterogeneity. Assumptions of independence and homogeneity of variance were checked with plots of residuals. The assumption of normality of residuals was checked with histograms of residuals for each test.

Analysis at the beta scale comparing beetle community turnover and deadwood structure turnover among forest sites in relation to disturbance history class was carried out by non-metric multidimensional scaling (NMS) (see Clark 1993) and SIMPER and ANOSIM analyses in Primer 5 2002 (PRIMER-E Ltd. 6 Hedingham Gardens, Roborough, Plymouth PL6 7DX, United Kingdom).

Secondly, multi-response permutation procedures (MRPP) were used to test whether beetle- and habitat-defined forests differed across disturbance history classes. This non-parametric analog to discriminate analysis circumvents assumptions of normality and homogeneity of variance that could not be met with the current data set. The MRPP method also returns the mean distance among sample points within each disturbance history class, which describes the relative heterogeneity among forests in each class.

For the distance measure in MRPP, we used the Sørenson coefficient (also known as the Czekanowski or Bray-Curtis coefficient). It measures percent dissimilarity (PD) between two samples, calculated as PD = 1–2W/A+B, where W is the sum of shared abundances and A and B are the sums of abundances in individual sample units.

For analysis at the gamma scale, species-sample curves were constructed to test the prediction that cumulative species richness for all naturally disturbed forests (fire and wind disturbed forests inclusive) was higher than that for all forests under even-age management (clearcut and thinned forests inclusive). Species-sample curves were also constructed individually for each disturbance history class to allow a visual evaluation of the gamma richness trends for each.

Statistical analyses were carried out with SYSTAT Version 5.02 (Systat Inc. 1993), S-PLUS (MathSoft 1999)and PC-ORD Version 3.09 (McCune and Mefford 1997).

Results

A total of 12,151 beetles of 389 species were collected. Of these, 296 species comprising 10,488 specimens in 45 families were determined to be saproxylic species (Appendix 1). Two species, *Anapsis rufa* Say and *Isomira quadristriata* (Cooper) were caught at all 30 sites and were the most abundant with 3,880 and 1,129 specimens respectively. Eighty-five species were represented by single captures and 216 species were represented by less than 10 specimens.

Forest structure generally showed high variation within disturbance history classes. Significant disturbance-class differences tested by a Kruskal-Wallis analysis were identified for 2 (CROWN X^2=10.54, p= 0.015, SIZE1 X^2=8.36, p=0.039, and marginally DECAY2 X^2=6.34, p=0.07) of the 12 variables tested. Crown closure (CROWN) was highest in wind disturbed and clearcut forests and lowest in fire disturbed forests. Small-diameter deadwood (SIZE1) showed significantly higher volumes in thinned forests than in either clearcut or wind disturbed forests. DECAY2 was greatest in WIND disturbed sites.

Stand age was not a function of any of the deadwood measures among stands.

Alpha diversity. The ANOVA analysis to test whether naturally disturbed forests exhibited higher diversity of deadwood structures offered evidence for one of the five attributes tested. SHAN-DECAY (diversity of deadwood decay classes in each forest) was significantly higher in both fire (p=0.040) and wind (p=0.004) disturbed forests than in thinned forests (F=4.75, p=0.01).

The general linear regression models constructed to determine whether the beetle diversity could be explained by habitat diversity attributes with disturbance class and age as factors resulted in four models (Table 3).

In interpreting these results, it should be borne in mind that the dependant variable is a function of the explanatory variables. If the coefficients are negative, the dependant variable is a negative function of the explanatory variable, and if positive a positive function. The F statistic represents the full model and the T/P are the univariate results.

Beta diversity. The forest sites plotted in the space of the beetle assemblage show two important patterns: differences in the inter-site distances within disturbance classes and actual segregation of forest disturbance classes (Figure 1, Table 4). Clearcut forests show the tightest aggregation (mean distance = 0.421), followed by fire disturbed forests (mean distance = 0.571), then thinned forests (mean distance = 0.581), with wind disturbed forests showing the greatest heterogeneity (mean distance = 0.603) which was statistically significant (Table 4).

Different beta patterns were observed in forests with regard to habitat structures. Figure 1 shows that, unlike the species-defined plot, fire disturbed forests show the

Table 3. Significant multiple linear regression models of beetle assemblage attributes (dependent variables) regressed against habitat structure diversity attributes (explanatory variables). Construction by forward and backward stepwise inclusion and exclusion of variables, based on two-tailed p-value of 0.1. T is the test statistic; P is the probability value.

Dependent Variable	Explanatory Variable(s)	Coefficient ±SE	T/P (2-tailed)	F-statistic	Model P-Value	Multiple R^2
ABUNDANCE	Intercept	-216.74±163.13	-1.33 / 0.20	3.95	0.01	0.29
	AGE	1.28±0.97	1.32 / 0.20			
	DIST. CLASS	10.72±36.69	0.29 / 0.77			
	SIZE1	1778.44±574.00	3.01 / 0.005			
	SHAN-D/C	584.43±186.75	3.12 / 0.004			
RICH/ABUN	Intercept	0.28±0.04	6.87 / 0.00	4.42	0.005	0.37
	AGE	0.00±0.00	-1.85 / 0.08			
	DIST. CLASS	0.01±0.01	1.02 / 0.32			
	SIZE1	-0.61±0.17	-3.48 / 0.00			
	SIZE2	0.33±0.14	2.27 / 0.03			
	DECIDUOUS	-0.14±0.06	-2.64 / 0.01			
SHANNON	Intercept	3.82±0.40	9.65 / 0.00	3.24	0.03	0.24
	AGE	-0.00±0.00	-1.94 / 0.06			
	DIST. CLASS	0.07±0.09	0.81 / 0.42			
	SIZE1	-4.36±1.39	-3.13 / 0.00			
	SHAN-D/C	-1.00±0.45	-2.21 / 0.04			
RARE-10	Intercept	68.96±10.89	6.35 / 0.00	2.17	0.10	0.10
	AGE	0.05±0.05	1.00 / 0.33			
	DIST. CLASS	-0.03±1.81	-0.02 / 0.99			
	CROWN	-27.91±13.44	-2.08 / 0.05			
	DECIDUOUS	47.62±22.90	2.08 / 0.05			

Table 4. Results of multi-response permutation procedures (MRPP) analysis, testing for separation of disturbance history classes based on (A) beetle assemblage and (B) forest habitat structures. Mean distance within class can be read as a relative measure of beta heterogeneity within disturbance history classes. P-values associated with multiple comparisons denote significance of group separation. Adjusted multiple comparison a level for p-value significance at 0.05 = 0.009, and for significance at 0.10 = 0.017, based on adjusted a = $1-(1-\alpha)^{1/\text{number of comparisons}}$

	CLEARCUT	CC-THINNED	FIRE	WIND	All-groups p-value
(A) mean distance within class	0.421	0.581	0.571	0.603	
CC&THINNED	0.027				
FIRE	0.001	0.075			0.0006
WIND	0.005	0.062	0.025		
(B) mean distance within class	0.217	0.296	0.353	0.175	
CC&THINNED	0.219				
FIRE	0.246	0.754			0.097
WIND	0.147	0.060	0.078		

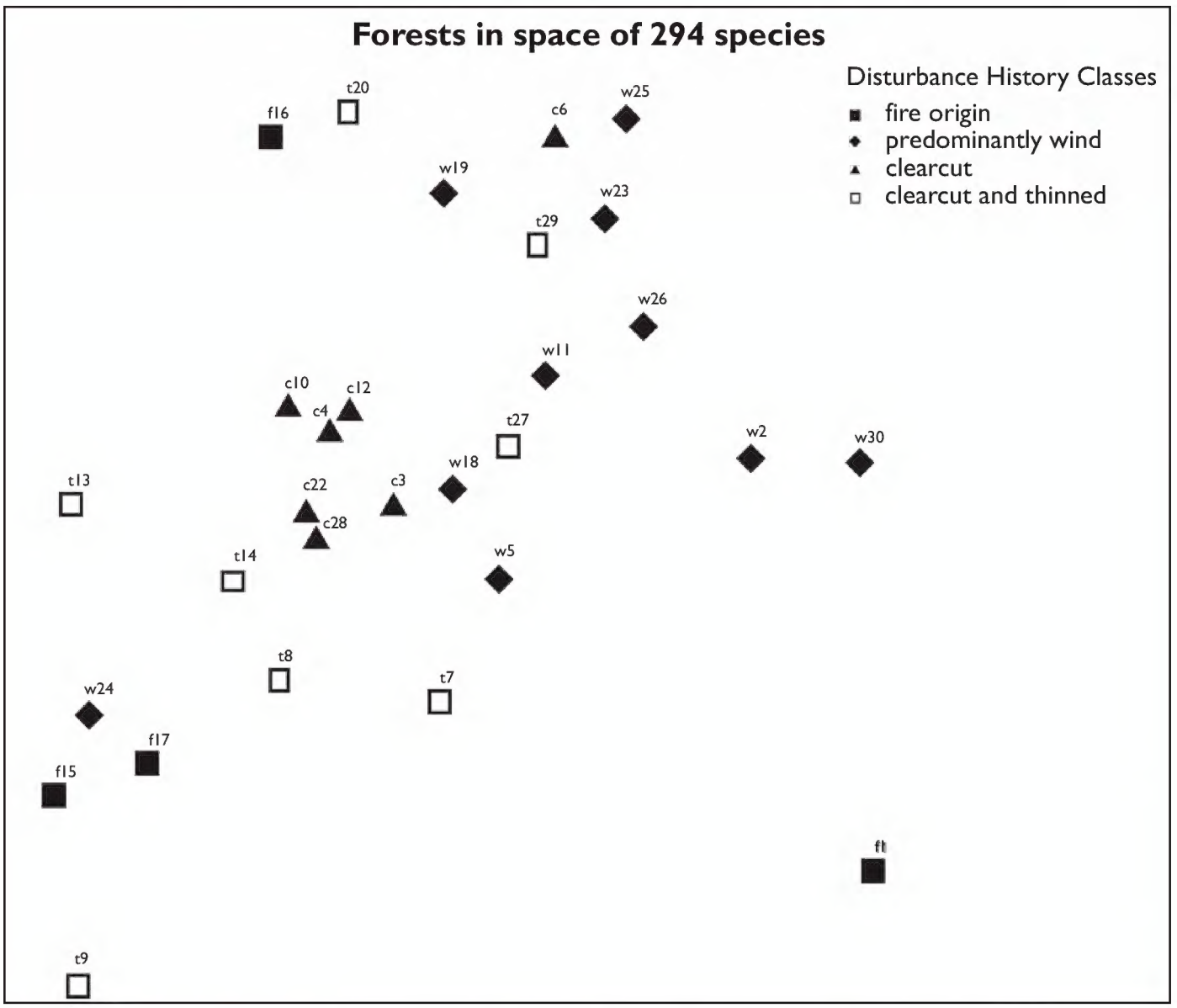

Figure 1. Non-metric multidimensional scaling ordination diagrams of forest sites in two-dimensional space defined by (A) beetle assemblage and (B) habitat structures. Symbols signify disturbance history class of forests: ▲= CLEARCUT, □= THINNED, ■= FIRE, and ◆= WIND. Numbers identify the specific forest. Forest number 25 was excluded as an outlier in (B) due to much higher deadwood volumes than all other sites.

greatest heterogeneity (mean distance = 0.353), followed by thinned forests (mean distance = 0.296) and then clearcut forests (mean distance = 0.217), and wind disturbed forests with the lowest heterogeneity (mean distance = 0.175) but the statistical difference was only significant at the 0.1 probability level (Table 4B). However, one must note that an outlying wind disturbed site (number 25) had an extremely high volume of deadwood and was removed due to difficulty in interpreting the NMS diagram otherwise. The MRPP for wind-disturbed forests, when the outlier was included, ranked the wind-disturbed class as second most heterogeneous, behind fire-disturbed forests.

The ANOSIM analysis testing for pair-wise similarities among disturbance classes gave a global R statistic of 0.174 with p=0.09 but none of the pair-wise R values were significant even at p=0.10. Results of the SIMPER analysis on average dissimilarity among pairs of sites by disturbance are presented in Appendix 2.

Gamma diversity. Of the 296 native saproxylic species sampled, 227 (77.2%) were sampled in the naturally disturbed forests and 228 (77.6%) were sampled in the managed forests. The first and second order Jackknife estimates of total species richness were 301.7 and 337.2 for naturally disturbed forests and 308.3 and 351.4 for managed forests. This does not support the prediction that the total fauna richness would be higher in naturally disturbed forests; in fact, the opposite appears more likely to be true. The species-sample curves constructed for the four disturbance classes (Figure 2)

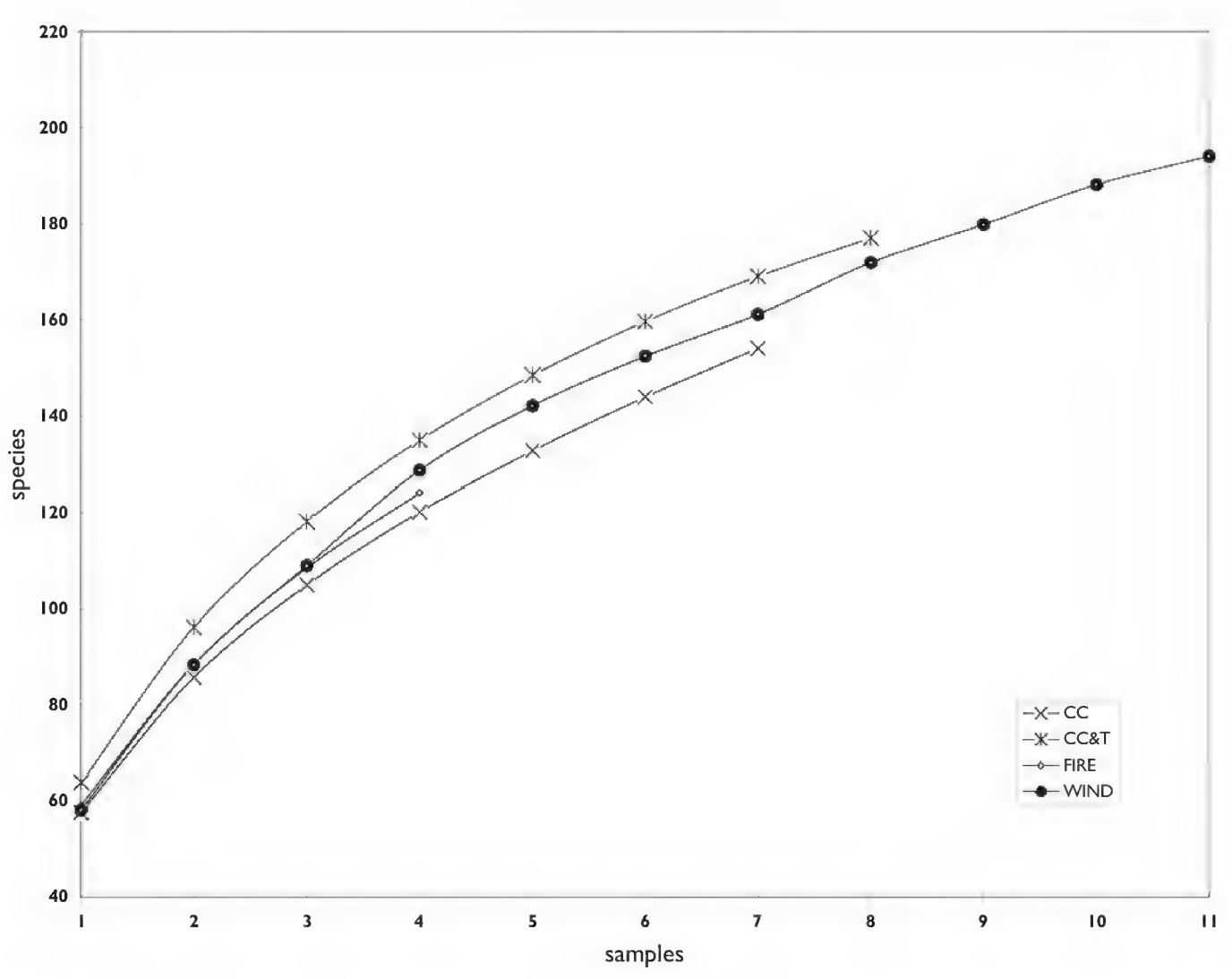

Figure 2. Species-sample curves for each forest disturbance class.

suggest the following relationship of species richness across disturbance history classes: thinned>wind>fire>clearcut.

Discussion

4.1 Alpha diversity. The analysis of deadwood structure and diversity at the alpha level revealed two insights about thinned forests: there is both a higher volume of small-diameter deadwood and a lower decay-class diversity in thinned forests compared to wind and fire disturbed forests. Both pre-commercial and commercial thinning treatments were represented in the thinned forest class (five and three forests, respectively). While thinning treatments are applied to stands of varying ages, the results are typically an immediate increase in the volume of similar-diameter downed deadwood. One would predict that this would lead to local homogeneity of deadwood size-structure, though this finding was not supported in our results. The senescence of the downed deadwood in a single cohort predictably results in decreased decay variation in space, as supported by the lower decay-class diversity in thinned forests. The higher volume of small-diameter deadwood in thinned forests probably reflects the dominance of pre-commercial thinning in the thinned class, because pre-commercial treatments are applied in forests with young, small trees. Thus, our results suggest that lower diversity and increased volumes of deadwood may be generally associated with the thinning practice.

Saproxylic beetle abundance was a positive function of small diameter deadwood volume and the diversity of total deadwood volume. Diversity of saproxylic beetles measured as richness divided by abundance, however, was a negative function of small diameter deadwood and deciduous deadwood but a positive function of intermediate size deadwood. Shannon diversity of saproxylic beetles was a negative function of the diversity deadwood (deciduous or coniferous) volume. Thus the relationships are not clear. Rare beetles were a negative function of crown closure and a positive function of deciduous deadwood volume.

One *post hoc* observation is worthy of mention: deadwood diversity levels in the managed forests might largely be an artifact of pre-harvest forest environments. Nearly all managed forests in this study were in their first or second even-age rotations. Hence, most of these forests likely contained large amounts of residual deadwood from deciduous species and large diameter trees, patterns one would not expect to endure through continued successive short-term rotations. Since second growth forests will usually be harvested before they can reproduce their own old-forest characteristic structures, we can only anticipate their eventual disappearance. In so much as these decomposing artifacts are microhabitats and resources, we can of course also anticipate the disappearance of the species that depend on them.

One explanation for the lack of clear results may be that deadwood may not have been measured over an area that was adequate to reflect any deterministic influences on local beetle assemblages. One cannot necessarily assume that a sampled array of flying beetles will reflect only the microhabitats available within a few hundred meters of

the sample points. In theory, the deadwood sampling area that is ideal for discerning relationships emerges from a combination of 'best' areas for individual species and individual forests. In recognizing this quandary of FIT sampling, Økland (1996) tested the habitat relationships for individual beetle species in Norway and found that habitat measurements collected over an area of 32 hectares produced the highest number of relationships. To assume that the measurements in this study represented the surrounding forest environment over this large an area may be unreasonable.

In a study comparing FIT sampling to bark-peeling as methods of determining saproxylic faunas, Siitonen (1994) found that the numbers of species and individuals of aerially-dispersing beetles captured by FITs were unaffected by the quantities of deadwood in the local area of the trap. He interpreted this to mean that the distribution of such aerially dispersing species was related to larger forest scales and not the immediate local conditions. Since the present study employed FITs, the beetle assemblages sampled may have been reflective of such larger forest scales. Gibb et al. (2006) found that saproxylic insects trapped using emergence traps showed a poor relationship with deadwood at local scales. Thus, in the future a combination of FIT and emergence trapping should probably be employed and larger stands, if available, should be sampled. Other techniques such as baited Lindgren funnel traps, bark peeling, car nets, hand collecting, and light-trapping may also yield beetles, particularly rare species, not sampled by conventional techniques (Muona 1999).

Beta diversity. While the alpha and gamma analyses focus on the unqualified diversities of habitats and beetle assemblages, within forests and within disturbance classes, the beta analyses examine the relative composition of the beetle assemblages and deadwood structures. The beta analyses revealed that actual species compositions of the assemblages were not clearly different among classes, and that higher turnover among naturally disturbed forests was evident. Observations of high turnover of saproxylic beetle species without changes in species richness were made in central Finland by Kaila et al. (1997) when comparing recent clearcuts with mature forests; by Väisänen et al. (1993) when comparing the fauna of birch trunks in old-growth forests with those in managed forests; and by Sippola et al. (2002) in comparing saproxylic beetle diversity in old growth and clearcut regeneration stands in Finnish Lapland. While the current study does not support the prediction of reduced species diversity related to reduced deadwood habitat diversity in managed forests, it does support the claim that managed forests support different faunal assemblages (Niemelä 1997).

The larger heterogeneity of fire disturbed forests is in keeping with studies that indicate that many saproxylic species are adapted to fire disturbances and subsequent forest succession (Granström 2001; Buddle et al. 2006). Siitonen (2003) identified the virtual elimination of fire disturbances in Fennoscandian boreal forests as one of two principal conservation concerns for saproxylic species (the other being the low proportion of old growth forests). Similarly, in relation to wind-disturbed forests, Duelli et al. (2002) documented dramatic short-term (over the span of a decade) increases in the species richness and biodiversity of invertebrates, reptiles, and small mammals in severe windthrow sites in Switzerland following a 1990 storm. At these same sites Wermelinger et al. (2002) found profound changes

in saproxylic beetles with certain groups (Cerambycidae and Buprestidae) becoming 30 to 500 times more abundant than in adjacent intact forests. Although the dramatic increases in numbers of individuals were relatively short-lived, the composition of the saproxylic beetle fauna became progressively more dissimilar from the control plots.

Gamma diversity. The final prediction of lower gamma diversity of saproxylic beetle species in managed forests compared to naturally disturbed forests was not supported. The prediction was partly underpinned by an assumption that forest habitat structures differed between managed and naturally disturbed forests at the alpha scale, which was not highly supported. If anything, the higher species-sample curve in thinned forests seems to suggest that thinning disturbance generates more species than either wind of fire disturbance. Otherwise, the non-thinned clearcut forests appeared to have a lower diversity of species than both wind and fire origin forests.

In Swedish forests Larsson et al. (2006) found that 'new forestry' management practices that left large volumes of deadwood in stands improve conditions for some species of saproxylic beetles. Furthermore saproxylic beetles as a group are a composite, reflective of different stages of wood decay. Sippola et al. (2002) examined saproxylic and non-saproxylic beetle diversity in old-growth and regeneration forests in Finland. Although no significant differences were detected in the rarefied number of species between old-growth and regeneration stands, the species composition of both saproxylic and non-saproxylic beetles differed. Species colonizing recently dead trees, soil-dwelling open-habitat species, and some polypore-dwelling ciids were more abundant in recently cut and regenerating sites, whereas many mycetophagous beetle families were almost completely absent. Overall saproxylic species richness or even species diversity does not discriminate between these different saproxylic components and may mask important differences between forest beetle communities in forest stands of different age, composition, or stand history.

Conservation requirements. The general claim that modern forestry in northern forests has altered invertebrates by altering forest habitat structure is well supported in the literature (Niemelä, 1997; Martikainen et al. 1999, 2000; Siitonen 2001; Grove 2002; Jonsson et al. 2005). In Nova Scotia, Dollin et al. (2008) found that harvested forest stands had lower Coleoptera species richness and were host to a significantly different suite of species than unharvested stands. Two tentative conclusions from the current study help extend this claim in Nova Scotia forests: 1) the species assemblage of saproxylic beetle species differed between managed and naturally disturbed forests, and 2) these beetle assemblages are more variable among naturally disturbed forests than among managed forests. If management is to decrease the altering effect of forestry practices, the next requirement is to identify or confirm the particular aspects of forest structure that are being altered and that are in turn altering biodiversity (Essen et al. 1992; Swanson and Franklin 1992; Noss and Cooperrider 1994; Franklin 1995; Lubchenco 1995; Niemelä 1997; Siitonen 2001, 2003; Grove 2002; Langor et al. 2006).

Research from countries with longer histories of intensive forestry has revealed several cases of invertebrate endangerment due to loss of microhabitats found in deadwood or moribund trees. Some of these microhabitats are lost because they are found in tree species that are not economically desirable, like aspen (Siitonen and Martikainen 1994)

and beech (Nilsson and Baranowski 1997). Others are threatened because they are part of trees with large diameters, which are not maintained amid short-lasting even-age stand rotations (Økland et al. 1995; Nilsson et al. 1995; Siitonen and Saaristo 2000). These and other factors have lead to concern about the diversity of deadwood microhabitats in general, as defined by decay states, sizes, and tree species (Økland et al. 1995).

If the goal in managing forests in Nova Scotia is to maintain patterns of heterogeneity similar to those that arise after natural disturbances, the indication offered here by saproxylic beetles is that this goal is not being met. Majka (2007) examined 14 families, subfamilies, and tribes of saproxylic beetles in the Maritime Provinces of Canada and found 59 apparently rare species (representing ≤ 0.005% of specimens from the region) that comprise 33% of the 178 species within these groups. Majka (2007) proposed that this apparent scarcity of a large proportion of the saproxylic fauna might be due to the history of forest management practices in the region. If Nova Scotia has not yet suffered biodepletion to the extent of European forests, this may only reflect the fact that not enough time has passed for the deadwood lingering from old-forests in second-growth forests to fully return to soil.

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Appendix 1

List of saproxylic beetles found in the present study (Av. S, average species richness; S, species richness).

	Trophic Category	Disturbance Classes							
		Clearcut 11 stands		Clearcut + thin 8 stands		Fire origin 4 stands		Wind disturbance 8 stands	
		Av. S	S	Av. S	S	Av. S	S	Av. S	S
Aederidae									
Aderinae									
Vanonus wickhami Casey	Xylo	0	0	0.1	1	0.5	1	0.1	1
Anobiidae									
Anobiinae									
Hadrobergmus notatus (Say)	Xylo	0.6	1	0.5	4	1.8	2	1.5	5
Hemicoelus carinatus (Say)	Xylo	0	0	0	0	0	0	0.1	1
Microbregma e. emarginatum (Duftschmid) †	Xylo	0	0	0	0	0	0	0.3	2
Platybregmus canadensis Fisher	Xylo	0.1	1	0	0	0	0	0	0
Dorcatominae									
Caenocara oculata (Say)	Xylo	0	0	0.3	2	0	0	0	0
Dorcatoma falli White	Xylo	0	0	0.4	2	0	0	0.7	4
Dorcatoma pallicornis LeConte	Xylo	0	0	0.4	3	0.5	2	0.6	4
Sculptotheca puberula (LeConte)	Xylo	0	0	0	0	0	0	0.3	2
Ptiliinae									
Ptilinus ruficornis Say	Xylo	0	0	0.4	2	0	0	0	0
Buprestidae									
Buprestidae									
*Melanophila d. drummundi (*Kirby)	Xylo	0	0	0.1	1	0	0	0	0
Carabidae									
Harpaliinae									
Bradycellus nigriceps LeConte	Pred	0.1	1	0	0	0	0	0	0
Bradycellus nigrinus (Dejean)	Pred	0.1	1	0.3	2	0	0	0	0
Bradycellus semipubescens (Dejean)	Pred	0	0	0.3	2	0.5	2	0.1	1
Cymindis limbatus Dejean	Pred	0	0	0	0	0	0	0.1	1
Dromius piceus Lindroth	Pred	0.4	3	0.3	2	0	0	0.4	2
Syntomus americanus (Dejean)	Pred	0	0	0.1	1	0	0	0	0
Trechinae									
Bembidion mimus Hayward	Pred	0	0	0.1	1	0	0	0	0
Trechus rubens (Fabricius) †	Pred	0.1	1	0	0	0	0	0	0
Cerambycidae									
Aseminae									
Asemum striatum (Linnaeus)	Xylo	0	0	0.3	1	0	0	0	0
Tetropium cinnamopterum (Kirby)	Xylo	0.1	1	0	0	0	0	0	0

	Trophic Category	Disturbance Classes							
		Clearcut 11 stands		Clearcut + thin 8 stands		Fire origin 4 stands		Wind disturbance 8 stands	
		Av. S	S	Av. S	S	Av. S	S	Av. S	S
Cerambycinae									
Molorchus b. bimaculatus Say	Xylo	0	0	0.1	1	0	0	0	0
Phymatodes testaceus (Linnaeus) †	Xylo	0.1	1	0	0	0	0	0.1	1
Laminae									
Hyperplatys maculata Haldeman	Xylo	0	0	0	0	0	0	0.1	1
Monochamus s. scutellatus (Say)	Xylo	0	0	0.1	1	0	0	0	0
Pogonocherus penicillatus LeConte	Xylo	0.1	1	0.3	2	0	0	0	0
Lepturinae									
Acmaeops p. proteus (Kirby)	Xylo	0	0	0	0	0.3	1	0	0
Acmaeopsoides rufulus (Haldeman)	Xylo	0	0	0	0	0.3	1	0	0
Anthophylax attenuatus (Haldeman)	Xylo	0	0	0	0	0	0	0.2	2
Anthophylax cyaneus (Haldeman)	Xylo	0	0	0	0	0	0	0.2	2
Anthophylax viridis LeConte	Xylo	0.1	1	0.6	3	0.3	1	0.3	2
Evodinus m. monticola (Randall)	Xylo	1.3	5	1.6	6	2	2	1.5	9
Idiopidonia pedalis (LeConte)	Xylo	2.1	4	2.1	5	0.8	1	0.4	4
Judolia m. montivagens (Couper)	Xylo	0	0	0.5	1	0	0	0.3	3
Leptura subhamata Randall	Xylo	0.1	1	0.4	3	2.5	3	0.3	3
Lepturobosca chrysocoma (Kirby)	Xylo	0	0	0.8	1	0.3	0	0	0
Pidonia rufficollis (Say)	Xylo	5.7	4	28.6	5	2.8	3	7.1	5
Stictoleptura c. canadensis (Olivier)	Xylo	0	0	0	0	0.3	1	0.1	1
Strangalepta abbreviata (Germar)	Xylo	1.7	5	5	7	2	3	3.5	8
Trachysida aspera brevifrons (Howden)	Xylo	0.1	1	0	0	0.3	1	0	0
Trachysida mutabilis (Newman)	Xylo	0	0	0.3	2	0	0	0	0
Xestoleptura tibialis (LeConte)	Xylo	0	0	0	0	0	0	0.1	1
Cerylonidae									
Cerylonidae									
Cerylon castaneum Say	Myceto	1.7	6	3.6	6	3.3	3	2.7	9
Ciidae									
Ciidae									
Ceracis sallei (Mellié)	Bolito	0	0	0.3	2	0	0	0	0
Ceracis thoracicornis (Ziegler)	Bolito	0	0	0	0	0.3	1	0	0
Cis fuscipes Mellié	Bolito	0.1	1	0	0	0	0	0	0
Cis horridulus Casey	Bolito	0	0	0	0	0	0	0.1	1
Orthocis punctatus (Mellié)	Bolito	0.4	2	2.3	6	0	0	0.1	1
Clambidae									
Clambus pubescens Redtenbacher *	Myceto	1.6	6	2	7	0.3	1	3.3	7
Cleridae									
Clerinae									
Thanasimus undatulus (Say)	Pred	0.3	1	0	0	0.3	1	0.1	1
Epiphloeinae									
Madoniella dislocata (Say)	Pred	0	0	0	0	0	0	0.1	1

	Trophic Category	Disturbance Classes							
		Clearcut 11 stands		Clearcut + thin 8 stands		Fire origin 4 stands		Wind disturbance 8 stands	
		Av. S	S	Av. S	S	Av. S	S	Av. S	S
Corylophidae									
Orthoperinae									
Orthoperus suturalis LeConte	Myceto	0.1	1	0.1	1	0.5	2	0.1	1
Cryptophagidae									
Atomariinae									
Atomaria fuscata Schönherr	Myceto	0	0	0.1	1	0	0	0	0
Atomaria lederi Johnson	Myceto	1.9	7	1.3	5	0.4	2	1.2	5
Atomaria nigrirostris Say	Myceto	0	0	0	0	0	0	0.1	1
Atomaria testacea Stephens	Myceto	0.4	3	0.6	4	0.1	1	0.4	3
Cryptophaginae									
Caenoscelis basalis Casey	Myceto	0	0	0.1	1	0	0	0	0
Cryptophagus mainensis Casey	Myceto	0	0	0	0	0	0	0.3	2
Henoticus serratus (Gyllenhal)	Myceto	0.1	1	0	0	0	0	0	0
Henotiderus obesulus (Casey)	Myceto	0.9	3	0.4	3	0.3	1	0.3	3
Pteryngium crenatum (Gyllenhal) †	Myceto	0	0	0	0	0	0	0.1	1
Cucujidae									
Cucujus c. clavipes Fabricius	Pred	0.1	1	0	0	0	0	0	0
Curculionidae									
Cossoninae									
Carphonotus testaceus Casey	Xylo	0	0	0.1	1	0	0	0.1	1
Himatium errens LeConte	Xylo	0	0	0.1	1	0.3	1	0	0
Scolytinae									
Conophthorus coniperda (Schwarz)	Xylo	0	0	0	0	0.3	1	0	0
Cryphalus r. ruficollis Hopkins	Xylo	0.6	4	0.8	3	3	4	0.7	5
Crypturgus borealis Swaine	Xylo	0.9	4	1.1	5	1.8	2	0.5	3
Crypturgus pusillus (Gyllenhal) †	Xylo	0	0	0	0	0.3	1	0	0
Dendroctonus rufipennis (Kirby)	Xylo	0	0	0.1	1	0	0	0.3	3
Dryocoetes affaber (Mannerheim)	Xylo	0.1	1	0	0	0	0	0.1	1
Dryocoetes autographus (Ratzeburg)	Xylo	1.1	4	0.3	2	0.3	1	0.7	6
Dryocoetes betulae Hopkins	Xylo	0.7	2	0.3	1	0	0	0.7	5
Hylurgops rugipennis pinifex (Fitch)	Xylo	0	0	0	0	0.5	1	0	0
Monarthrum mali (Fitch)	Xylo	0	0	0.1	1	0.3	1	0	0
Pityogenes hopkinsi Swaine	Xylo	0.1	1	0.1	1	0.8	2	0.3	2
Pityokteines sparsus (LeConte)	Xylo	0.1	1	0.3	2	0.3	1	0	0
Pityophthorus balsameus Blackman	Xylo	0.1	1	0.3	2	0.5	2	0	0
Pityophthorus biovalis Blackman	Xylo	0	0	0.3	1	0	0	0.1	1
Pityophthorus dentifrons Blackman	Xylo	0	0	0.4	2	0	0	0.2	2
Pityophthorus nitidus Swaine	Xylo	0	0	0	0	0.3	1	0	0
Pityophthorus opaculus LeConte	Xylo	0	0	0	0	1	2	0.1	1
Pityophthorus puberulus (LeConte)	Xylo	0	0	0.1	1	1	2	0.1	1
Polygraphus rufipennis (Kirby)	Xylo	0.6	2	2	2	2.3	4	0.5	4

	Trophic Category	Disturbance Classes							
		Clearcut 11 stands		Clearcut + thin 8 stands		Fire origin 4 stands		Wind disturbance 8 stands	
		Av. S	S	Av. S	S	Av. S	S	Av. S	S
Trypodendron betulae Swaine	Myceto	0	0	0	0	0.5	1	0.6	2
Trypodendron lineatum (Olivier) *	Myceto	1	4	1.3	5	1.8	3	1.1	7
Trypodendron rufitarsus (Kirby)	Myceto	1.7	5	0.8	4	1.5	3	0.5	3
Xyleborus sayi (Hopkins)	Myceto	0.4	3	0	0	0.3	1	0.2	2
Xylechinus americanus Blackman	Xylo	0	0	0.1	1	0	0	0.3	3
Xyloterinus politus (Say) *	Myceto	0.4	3	0.4	2	0.8	1	0.5	6
Elateridae									
Elaterinae									
Ampedus deletus (LeConte)	Xylo	1.9	6	3	5	3.8	4	1.6	8
Ampedus fusculus (LeConte)	Xylo	0	0	0.1	1	0	0	0	0
Ampedus laesus (LeConte)	Xylo	0	0	0.1	1	0			
Ampedus luctuosus (LeConte)	Xylo	0	0	0.5	3	1	3	0.5	4
Ampedus mixtus (Herbst)	Xylo	0.1	1	0.3	2	2.5	3	0	0
Ampedus protervus (LeConte)	Xylo	0.1	1	0.1	1	0	0	0	0
Ampedus pullus Germar	Xylo	0	0	0	0	0.3	1	0.1	1
Ampedus semicinctus (Randall)	Xylo	0	0	0	0	0.3	1	0	0
Ampedus sp. undescribed	Xylo	0.1	1	0	0	0	0	0	0
Dalopius cognatus Brown	Myceto	3.7	4	3	2	9.8	4	3.5	6
Dalopius fuscipes Brown	Myceto	0	0	0.1	1	0	0	0.3	2
Dalopius gentilis Brown	Myceto	0.7	1	0.1	1	0.3	1	5.6	4
Dalopius pennsylvanicus Brown	Myceto	0	0	0.1	1	0	0	0	0
Dalopius vagus Brown	Myceto	4.6	2	4.3	4	3	1	0.1	1
Prosterninae									
Athous brightwelli (Kirby)	Pred	0.1	1	0	0	0	0	0.3	2
Athous orvus Becker	Pred	0	0	0	0	0.3	1	0.3	2
Athous rufifrons (Randall)	Pred	4.4	6	5.3	7	0.5	2	1.9	8
Athous scapularis (Say)	Pred	0	0	0	0	0	0	0.1	1
Beckerus appressus (Randall)	Pred	0.1	1	0	0	0	0	0	0
Denticollis denticornis (Kirby)	Pred	2.4	6	8.9	8	1	3	1.8	9
Eanus maculipennis (LeConte)	Pred	0	0	0.8	2	0	0	0	0
Hypoganus sulcicollis (Say)	Pred	0	0	0	0	0			
Liotrichus falsificus (LeConte)	Pred	2.9	7	2.8	7	3.8	3	2.7	8
Liotrichus spinosus (LeConte)	Pred	3.7	7	3.9	8	7	4	2.5	8
Liotrichus vulneratus (LeConte)	Pred	0	0	0.5	2	0.3	1	0.2	2
Nitidolimonius resplendens (Randall)	Pred	0.6	2	0.1	1	0			
Metanomus insidiosus (LeConte)	Pred	1.7	5	3.4	6	1.3	2	1.1	5
Oxygonus montanus Schaeffer	Pred	0.6	3	1.1	3	0	0	1.7	5
Pseudanostirus hamatus (Say)	Pred	0	0	0.1	1	0			
Pseudanostirus p. propolus (LeConte)	Rhizo/ Pred	0	0	0	0	0.3	1	0.5	5
Pseudanostirus triundulatus (Randall)	Rhizo/ Pred	4.9	6	8.1	7	5.5	4	6.1	11

	Trophic Category	Disturbance Classes							
		Clearcut 11 stands		Clearcut + thin 8 stands		Fire origin 4 stands		Wind disturbance 8 stands	
		Av. S	S	Av. S	S	Av. S	S	Av. S	S
Setasomus nitidulus (LeConte)	Pred	0.4	3	0.5	2	0.8	2	0.2	2
Setasomus rufopluralis (Fall)	Pred	0	0	0	0	0	0	0.2	2
Sylvanelatyer cylindriformis (Herbst)	Pred	0	0	0.1	1	0			
Endomychidae									
Epipocinae									
Hadromychus chandleri B & L	Myceto	0.3	1	0	0	0	0	0	0
Lycoperdininae									
Mycetina perpulchra (Newman)	Myceto	0.4	3	0.6	3	0.3	1	0.2	2
Merophysinae									
Phymaphora pulchella Newman	Myceto	0.3	2	0.5	3	0	0	0.1	1
Erotylidae									
Tritominae									
Triplax dissimulator (Crotch)	Bolito	0	0	0	0	0.5	1	0	0
Triplax flavicollis Lacordaire	Bolito	0	0	0	0	0	0	0.1	1
Tritoma pulchra Say	Bolito	1.1	5	2.1	3	0.5	1	0.6	6
Eucinetidae									
Eucinetus morio LeConte	Myceto	0	0	0.4	2	0	0	0.2	1
Nycteus punctulatus (LeConte)	Myceto	0	0	0	0	0	0	0.1	1
Eicnemidae									
Melasinae									
Epiphanis cornutus Eschscholtz	Myceto	0.1	1	1	3	0.8	2	0.4	3
Hylis terminalis (LeConte)	Myceto	0.4	2	0	0	0	0	0	0
Isorhipis obliqua (Say)	Myceto	0.1	1	0.3	2	0	0	0	0
Microrhagus pectinatus (LeConte)	Myceto	0	0	0.1	1	0.3	1	0.1	1
Histeridae									
Dendrophilinae									
Paromalus teres LeConte	Pred	0.1	1	0.3	2	0	0	0.1	1
Laemophloeidae									
Laemophloeinae									
Laemophloeus fasciatus Melsheimer	Myceto	0	0	0	0	0	0	0.1	1
Lampyridae									
Lampyrinae									
Ellychnia corrusca (Linnaeus)	Pred	3	7	4.4	8	2.8	4	2.8	10
Lucidota atra (Olivier)	Pred	0	0	0.1	1	0	0	0.1	1
Pyractomena angulata (Say)	Pred	0.1	1	0.5	1	0.5	1	0.1	1
Latridiidae									
Cortcariinae									
Corticaria species	Myceto	0.1	1	0.5	3	0.3	1	0.3	2
Cortinicara gibbosa (Herbst) †	Myceto	0.1	1	0.6	3	1			
Melanophthalma americana Mannerheim	Myceto	0.6	2	0.6	1	10	4	0.7	5

	Trophic Category	Disturbance Classes							
		Clearcut 11 stands		Clearcut + thin 8 stands		Fire origin 4 stands		Wind disturbance 8 stands	
		Av. S	S	Av. S	S	Av. S	S	Av. S	S
Melanophthalma inermis Motshulsky	Myceto	0.1	1	0	0	0	0	0	0
Melanophthalma pumila (LeConte)	Myceto	9.4	6	25.1	8	89.5	4	12	11
Latridiinae									
Cartodere constricta (Gyllenhal) †	Myceto	0	0	0	0	0.5	2	0	0
Enicmus tenuicornis LeConte	Myceto	0.9	5	1.6	6	1.3	3	2.5	10
Latridius minutus (Linnaeus) †	Myceto	0.1	1	0.3	2	0	0	0.2	2
Stephostethus liratus (LeConte)	Myceto	0.4	2	0.1	1	0	0	0.3	3
Leiodidae									
Leiodinae									
Agathidium difformis (LeConte)	Bolito	0	0	0.4	2	0			
Agathidium fawcettae Miller & Wheeler	Bolito	7.3	7	2.4	7	2.3	3	5.3	10
Anisotoma basalis (LeConte)	Bolito	0	0	0.1	1	0	0	0.2	2
Anisotoma blanchardi (Horn)	Bolito	0	0	0	0	0	0	0.2	2
Anisotoma geminata (Horn)	Bolito	0	0	0	0	0	0	0.1	1
Anisotoma horni Wheeler	Bolito	0	0	0.3	2	0	0	0.1	1
Anisotoma inops Brown	Bolito	3.6	7	3.1	7	3	4	5.9	11
Leiodes assimilis (LeConte)	Bolito	0	0	0.1	1	0	0	0	0
Lucanidae									
Syndescinae									
Ceruchus piceus (Weber)	Xylo	0.1	1	0.3	2	0.3	1	0.2	2
Lycidae									
Erotinae									
Dictyopterus aurora (Herbst)	Myceto	1.3	3	4.4	6	1	2	2.4	10
Eros humeralis (Fabricius)	Myceto	0.4	2	0.4	2	0.5	2	0.3	3
Lycinae									
Leptoceletes basalis LeConte	Myceto	0.1	1	0.1	1	0.3	1	0.4	4
Platoderinae									
Plateros lictor (Newman)	Myceto	0.4	3	0.9	4	0.5	1	0.1	1
Plateros subfurcatus Green	Myceto	0.1	1	0	0	0	0	0	0
Melandryidae									
Melandryinae									
Dircaea liturata (LeConte)	Xylo	0.3	1	1.5	4	0.3	1	0.5	5
Emmesa connectans Newman	Xylo	0.7	4	0.5	3	0	0	0.5	3
Hypulus simulator (Newman)	Xylo	0	0	0	0	0	0	0.1	1
Orchesia castanea (Melsheimer)	Myceto	0.4	3	0.9	5	0.3	1	0.1	1
Prothalpia undata LeConte	Xylo	0.4	3	0.1	1	0	0	0.2	2
Scotochroa atra LeConte	Xylo	0.1	1	0	0	0	0	0.1	1
Scotochroa buprestoides (Kirby)	Xylo	0	0	0.4	2	0	0	0	0
Scotochroides antennatus Mank	Xylo	0.6	4	0.9	5	0.8	2	0.5	5
Serropalpus substriatus Haldeman	Xylo	0.7	2	0.8	6	0.5	2	0.6	2

	Trophic Category	Disturbance Classes							
		Clearcut 11 stands		Clearcut + thin 8 stands		Fire origin 4 stands		Wind disturbance 8 stands	
		Av. S	S	Av. S	S	Av. S	S	Av. S	S
Spilotus quadripustulatus (Melsheimer)	Xylo	0	0	0	0	0	0	0.1	1
Symphora flavicollis (Haldman)	Xylo	0.1	1	0	0	0	0	0.2	2
Xylita laevigata (Hellenius)	Xylo	0	0	0.3	2	0	0	0	0
Xylita livida (Sahlberg) *	Xylo	0	0	0	0	0.5	1	0	0
Monotomidae									
Rhizophaginae									
Rhizophagus dimidiatus Mannerheim	Pred	0.3	1	0	0	0.8	2	0.2	2
Mycetophagidae									
Mycetophaginae									
Mycetophagus pluripunctatus LeConte	Myceto	0	0	0	0	0	0	0.1	1
Nitidulidae									
Carpophilinae									
Carpophilus brachypterus (Say)	Sap	0	0	0	0	0.3	1	0	0
Cillaeinae									
Colopterus truncatus (Randall)	Sap	0	0	0.1	1	0	0	0.1	1
Cryptarchinae									
Glischrochilus fasciatus (Olivier)	Sap	0	0	0	0	1	1	0	0
Glischrochilus sanguinolentus (Olivier)	Sap	0.9	4	2.1	6	3.8	2	1.5	6
Glischrochilus siepmanni Brown	Sap	0	0	0	0	0.5	2	0	0
Epuraeinae									
Epuraea aestiva (Linnaeus)	Sap	0.6	2	0.8	2	0.3	1	0.2	2
Epuraea erichsonii Reitter	Sap	0.1	1	0	0	0	0	0	0
Epuraea labilis Erichson	Sap	1.1	6	1.9	6	1.5	4	0.8	6
Epuraea rufida (Melsheimer)	Sap	0	0	0	0	0.3	1	0	0
Epuraea terminalis Mannerheim	Sap	0.1	1	0	0	0	0	0	0
Epuraea truncatella Mannerheim	Sap	0	0	0.1	1	0.3	1	0.3	2
Oedemeridae									
Calopodinae									
Calopus angustus LeConte	Phloeo	0	0	0	0	0	0	0.2	2
Pyrochroidae									
Pyrochroinae									
Dendroides canadensis Latreille	Myceto	0.1	1	0.3	2	0	0	0	0
Dendroides concolor (Newman)	Myceto	0.1	1	0.6	2	0	0	0.1	1
Schizotus cervicalis Newman	Myceto	0.1	1	0.1	1	0	0	0	0
Pythidae									
Priognathus monilicornis (Randall)	Xylo	0.1	1	0.8	5	0.3	1	0.2	2
Salpingidae									
Salpinginae									
Salpingus viridiaeneus Randall	Xylo	0.1	1	0.1	1	0	0	0	0
Scarabaeidae									
Cetoniinae									

	Trophic Category	Disturbance Classes							
		Clearcut 11 stands		Clearcut + thin 8 stands		Fire origin 4 stands		Wind disturbance 8 stands	
		Av. S	S	Av. S	S	Av. S	S	Av. S	S
Trichiotinus assimilis (Kirby)	Xylo	0	0	0	0	0	0	0.1	1
Scirtidae									
Cyphon collaris (Guérin-Méneville)	Sap-P	0.9	2	0.8	5	1.3	3	0.8	4
Cyphon confusus (Brown) [1]	Sap-P	0.3	2	0.5	4	0.5	2	0.1	1
Cyphon obscurus (Guérin-Menéville) [1]	Sap-P	1	2	0.4	1	0.3	1	0.2	2
Cyphon ruficollis (Say)	Sap-P	0	0	0	0	0	0	0.1	1
Cyphon variabilis (Thunberg) *	Sap-P	0.3	2	0.4	2	0.5	1	0.5	1
Scraptiidae									
Anaspidinae									
Anaspis flavipennis Haldeman	Myceto	6.9	7	18	8	8	3	7.5	9
Anaspis nigrina Csiki	Myceto	0.3	1	0.6	3	0	0	0	0
Anaspis rufa Say	Myceto	88.3	7	125.8	8	175.5	4	141.3	11
Scraptiinae									
Canifa pallipes (Melsheimer)	Myceto	0.4	2	0	0	4.8	3	0.5	1
Canifa pusilla (Haldeman)	Myceto	1.4	3	2.9	6	5.8	4	3.7	8
Scydmaenidae									
Euconnus debilitans (Casey)	Pred	0.3	2	0	0	0	0	0	0
Euconnus testaceipes (Casey)	Pred	0.1	1	0	0	0	0	0.2	2
Stenichmus badius (Casey)	Pred	0.3	2	1.1	5	0.5	1	0.4	4
Silvanidae									
Brontinae									
Dendrophagus cygnaei Mannerheim	Myceto	0	0	0.3	2	0	0	0.1	1
Silvaninae									
Silvanus bidentatus (Fabricius) †	Myceto	0	0	0.1	1	0	0	0.4	2
Sphinididae									
Odontosphindinae									
Odontosphindus denticollis LeConte	Myxo	0	0	0	0	0	0	0.3	2
Sphinidinae									
Eurysphindus hirtus LeConte	Myxo	0	0	0.1	1	0	0	0	0
Sphindus trinifer Casey	Myxo	0.6	1	0	0	0	0	0.1	1
Staphylinidae									
Aleocharinae									
Amischa analis (Gravenhorst) †	Pred	0	0	0	0	0	0	0.2	2
Atheta brunswickensis Klimaszewski	Pred	0.1	1	0	0	0			
Atheta dadopora Thomson †	Pred	0	0	0.1	1	0			
Atheta hampshirensis (Bernhauer)	Pred	0	0	0	0	0			
Atheta klagesi Bernhauer *	Pred	0.1	1	0.3	2	0.5	1	0.5	3
Atheta pennsylvanica Bernhauer	Pred	0	0	0	0	0.3			
Atheta species 2	Pred	0.1	1	0.5	2	0.5	2	0.6	5
Atheta vetricosa Bernhauer	Pred	0	0	0.1	1	0	0	0	0
Deinopsis harringtoni Casey	Pred	0	0	0	0	0.3	1	0	0

		Trophic Category	Disturbance Classes							
			Clearcut 11 stands		Clearcut + thin 8 stands		Fire origin 4 stands		Wind disturbance 8 stands	
			Av. S	S	Av. S	S	Av. S	S	Av. S	S
	Gyrophaena species	Pred	0	0	0.1	1	0	0	0.1	1
	Leptusa brevicollis Casey	Pred	0.4	3	0.8	2	0.3	1	1.2	10
	Leptusa canonica Casey	Pred	0	0	0	0	0	0	0.1	1
	L*eptusa carolinensis* Pace	Pred	0.4	2	1.1	5	0.3	1	2.1	10
	L*eptusa gatineauensis* Klimaszewski	Pred	0	0	0	0	0	0	0.1	1
	Leptusa opaca Casey	Pred	0.4	3	0.6	3	0.8	3	0.5	4
	Mocyta breviscula (Mäklin)	Pred	0	0	0.1	1	0			
	Myllaena arcana Casey	Pred	0.1	1	0	0	0	0	0	0
	Oxypoda nicriceps Casey	Pred	0	0	0.1	1	0	0	0	0
	Philhygra species 1	Pred	0.1	1	0.1	1	0	0	0	0
	Philhygra species 2	Pred	0.1	1	0	0	0	0	0.1	1
	Phloeopora species	Pred	0	0	0	0	0	0	0.2	2
Omaliinae										
	Acidota crenata (Fabricius) *	Pred	0.1	1	0	0	0	0	0	0
	Hapalaraea hamata (Fauvel)	Pred	0.3	2	0	0	0	0	0.5	3
	Phloeonomus laesicollis (Mäklin)	Pred	0	0	0.1	1	0.5	2	0.3	3
Paederninae										
	Lithocharis thoracica (Casey)	Pred	0	0	0.1	1	0	0	0	0
	Palaminus hudsonicus Casey	Pred	0.1	1	0	0	0	0	0	0
	Scopaeus notangulus Casey	Pred	0.1	1	0	0	0	0	0	0
Phloeocharinae										
	Charyphus picipennis (LeConte)	Pred	0.1	1	0.1	1	0.3	1	0.2	2
Pselaphinae										
	Batrisodes lineaticollis (Aubé)	Pred	0.3	2	0.4	3	0.5	2	0.6	3
	Bibloplectus integer (LeConte)	Pred	0.3	1	0	0	0	0	0	0
	Bibloporus bicanalis (Casey)	Pred	0.9	4	1.4	4	1	2	1	5
	Euplectus duryi Casey	Pred	0	0	0	0	0	0	0.1	1
	Euplectus elongatus Brendel	Pred	0	0	0.3	2	0	0	0.1	1
	Reichenbachia spatulifer Casey	Pred	0.1	1	0	0	0	0	0	0
Scaphidinae										
	Baeocera congenera (Casey)	Myceto	0	0	0	0	0.5	1	0	0
	Scaphidium quadriguttatum Say	Myceto	0	0	0.1	1	0	0	0	0
	Scaphisoma lacustris Casey	Myceto	0.1	1	0.1	1	0.5	2	0.3	3
Staphylininae										
	Atrecus americanus (Casey)	Pred	0	0	0.1	1	0.3	1	0.3	3
	Atrecus macrocephalus (Nordmann)	Pred	0	0	0.3	2	0	0	0	0
	Bisnius blandus (Say)	Pred	0.1	1	0	0	0	0	0	0
	Erichsonius patella (Horn)	Pred	0.3	2	0	0	0	0	0	0
	Gabrius microphthalmus (Horn)	Pred	0.3	2	0.1	1	0	0	0.3	3
	Gabrius picipennis (Mäklin)	Pred	0	0	0.3	1	0	0	0.1	1
	Gyrohypnus cambelli Smetana	Pred	0.4	1	0.4	3	0.5	2	0.8	5

	Trophic Category	Disturbance Classes							
		Clearcut 11 stands		Clearcut + thin 8 stands		Fire origin 4 stands		Wind disturbance 8 stands	
		Av. S	S	Av. S	S	Av. S	S	Av. S	S
Ontholestes cingulatus (Gravenhorst)	Pred	0	0	0.1	1	0	0	0	0
Philonthus caeruleipennis Mannerheim	Pred	0	0	0	0	0	0	0.2	2
Platydracus cupripennis (Melsimer)	Pred	0	0	0.1	1	0	0	0	0
Platydracus viridanus Horn	Pred	0	0	0	0	0	0	0.1	1
Quedius canadensis (Casey)	Pred	0	0	0.1	1	0	0	0.1	1
Quedius capucinus (Gravenhorst)	Pred	0	0	0.1	1	0	0	0.2	2
Quedius curtipennis Bernhauer †	Pred	0.1	1	0.1	1	0	0	0.1	1
Quedius peregrinus (Gravenhorst)	Pred	0	0	0.1	1	0	0	0	0
Quedius plagiatus Mannerheim	Pred	0.1	1	0.3	1	0	0	0	0
Quedius rusticus Smetana	Pred	0.9	5	0.6	2	0.3	1	1.1	8
Tympanophorus puncticollis (Erichson)	Pred	0.3	2	0.3	1	0.3	1	0	0
Tachyporinae									
Bryophacis smetanai (Campbell)	Pred	0.1	1	0.5	3	0	0	0.3	2
Bryoporus rufescens LeConte	Pred	0.4	3	1.1	4	0	0	0.8	7
Lordithon quaesitor (Horn)	Pred	0	0	0.1	1	0	0	0	0
Mycetoporus consors LeConte	Pred	6.3	6	5.4	7	6.3	4	8.4	11
Sepedophilus cinctulus (Erichson)	Myceto	0	0	0	0	0	0	0.1	1
Sepidophilus crassus (Gravenhorst)	Myceto	0	0	0	0	0	0	0.3	1
Sepidophilus littoreus (Linnaeus) †	Myceto	0.4	2	0.1	1	0	0	0.3	2
Tachinus fumipennis (Say)	Pred	0	0	0	0	0	0	0.2	2
Tachinus luridus Erichson	Pred	0.1	1	0	0	0	0	0	0
Tachyporus dispar (Paykull) †	Pred	0	0	0	0	0	0	0.1	1
Tachyporus nitidulus (Fabricius) †	Pred	0.3	1	0	0	0	0	0.1	1
Stenotrachelidae									
Cephaloinae									
Cephaloon lepturoides Newman	Myceto	0	0	0	0	0	0	0.1	1
Cephaloon ungulare LeConte	Myceto	5.9	7	1.9	4	0.3	1	3	8
Tenebrionidae									
Alleculinae									
Capnochroa fuliginosa (Melsheimer)	Myceto	0.1	1	0	0	0	0	0.1	1
Hymenorus niger (Melsheimer)	Myceto	0.3	1	0.1	1	0	0	0.5	5
Isomira quadristriata (Couper)	Myceto	39.7	7	56.1	8	28.5	4	26.2	11
Mycetochara analis (LeConte)	Myceto	0.3	2	0	0	0.3	1	0	0
Mycetochara bicolor (Couper)	Myceto	0	0	0	0	0	0	0.2	2
Bolitophaginae									
Bolitophagus corticola Say	Bolito	0	0	0.1	1	0	0	0	0
Diaperinae									
Scaphidema aeneolum (LeConte)	Bolito	0	0	0	0	0	0	0.1	1

	Trophic Category	Disturbance Classes							
		Clearcut 11 stands		Clearcut + thin 8 stands		Fire origin 4 stands		Wind disturbance 8 stands	
		Av. S	S	Av. S	S	Av. S	S	Av. S	S
Lagrinae									
Paratenetus undescribed species	Sap-P	1	6	1.6	7	0.8	3	0.8	5
Tetratomidae									
Eustrophinae									
Eustrophus tomentosus Say	Bolito	0	0	0	0	0	0	0.1	1
Penthinae									
Penthe pimelia (Fabricius)	Bolito	0	0	0.4	2	0	0	0.1	1
Tetratominae									
Tetratoma tesselata Melsheimer	Bolito	0.1	1	0.1	1	0	0	0.1	1
Throscidae									
Throscinae									
Aulonothroscus constrictor (Say)	Myceto	3.1	5	8.9	6	2.3	3	2.8	10
Trixagus carinicollis (Schaeffer)	Myceto	0.4	3	0	0	0.3	1	0.4	2
Trogossitidae									
Peltinae									
Thymalus marginicollis Chevrolat	Bolito	0	0	0	0	0	0	0.1	1

1 Species of the genus *Cyphon* in the Maritime Provinces are presently being revised by Majka and Klausnitzer (in preparation). These species names may change in this forthcoming revision.

2 This undescribed species of *Paratenetus* (previously included within *Paratenetus fuscus* LeConte) will be described in a forthcoming publication by P. Bouchard and Y. Bousquet (in preparation).

Notes: Trophic Categories: Bolito, Bolitophagous; Myceto, Mycetophagous; Myxo, Myxomycophagous; Pred, Predaceous; Rhizo, Rhizophagous; Sapro, Saprophytic; SF, Sap Feeder; Xylo, Xylophagous. † indicates a Palaearctic species; * indicates a Holarctic species.

Appendix 2

SIMPER analysis showing average dissimilarity among sites by Disturbance Classes and the primary species of beetles involved.

Clearcut and Clearcut and Thinned

Average dissimilarity = 44.33

	Clear-cut	*CC &Thinned*				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
A. rufa	88.29	125.75	6.98	1.60	15.75	15.75
I. quadristriata	39.71	56.13	5.90	1.16	13.31	29.06
M. pumila	9.43	25.13	2.85	1.21	6.42	35.49
P. ruficollis	5.71	28.63	2.35	0.67	5.30	40.78

Clearcut and Fire Disturbance

Average dissimilarity = 54.51

	Clearcut	*Fire*				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
A. rufa	88.29	175.50	13.55	2.45	24.87	24.87
M. pumila	9.43	89.50	11.20	1.24	20.54	45.40
I. quadristriata	39.71	28.50	4.43	1.60	8.12	53.52

Clearcut and thinned and Fire Disturbed

Average dissimilarity = 58.09

	CC &Thinned	*Fire*				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
A. rufa	125.75	175.50	13.55	2.08	23.33	23.33
M. pumila	25.13	89.50	10.49	1.23	18.05	41.38
I. quadristriata	56.13	28.50	6.83	1.05	11.75	53.13

Clear-cut and Wind Disturbed

Average dissimilarity = 46.78

	Clearcut	Wind				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
A. rufa	88.29	141.27	9.82	1.51	21.00	21.00
I. quadristriata	39.71	26.18	4.34	1.81	9.28	30.28
M. pumila	9.43	12.00	2.84	1.10	6.07	36.36
P. ruficollis	5.71	7.09	1.89	0.96	4.04	40.39

Clear-cut and thinned and Wind Disturbed
Average dissimilarity = 51.12

	CC &Thinned	Wind				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
A. rufa	125.75	141.27	9.13	1.19	17.86	17.86
I. quadristriata	56.13	26.18	6.77	1.12	13.24	31.10
M. pumila	25.13	12.00	3.15	1.21	6.17	37.27
P. ruficollis	28.63	7.09	2.77	0.76	5.43	42.70
A. flavipennis	18.00	7.55	1.66	1.35	3.24	45.94

Fire and Wind Disturbed
Average dissimilarity = 57.64

	Fire	Wind				
Species	**Av.Abund**	**Av.Abund**	**Av.Diss**	**Diss/SD**	**Contrib%**	**Cum.%**
A. rufa	175.50	141.27	14.46	1.53	25.08	25.08
M. pumila	89.50	12.00	10.69	1.24	18.54	43.63
I. quadristriata	28.50	26.18	3.41	1.12	5.91	49.54

A. rufa = *Anaspis rufa*; *I. quadristriata* = *Isomira quadristriata; M. pumila* = *Melanophthalma pumila*; *P. ruficollis* = *Pidonia ruficollis*; *A. flavipennis* = *Anaspis flavipennis*.